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SOCIAL BEHAVIOR OF POLAR BEARS (URSUS MARITIMUS PHIPPS) CONCENTRATED ON LAND DURING THE ICE-FREE SEASON OF HUDSON BAY

University — Université

UNIVERSITY OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

MASTER OF SCIENCE

Year this degree conferred — Année d'obtention de ce grade

1980

Name of Supervisor — Nom du directeur de thèse

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SOCIAL BEHAVIOR OF POLAR BEARS (*URSUS MARITIMUS* PHIPPS) CONCENTRATED ON LAND DURING THE ICE-FREE SEASON OF HUDSON BAY

by

© PAUL B. LATOUR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

ZOOLOGY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Social Behavior of Polar Bears (*Ursus maritimus* Phipps) Concentrated on Land during the Ice-free Season of Hudson Bay submitted by Paul B. Latour in partial fulfilment of the requirements for the degree of Master of Science.

.....Ian O. Murie.....
Supervisor

.....

.....

.....

Date. 25 August 1980

THESIS ABSTRACT

Polar bears were observed at Cape Churchill, Manitoba, from 4 September to 19 November, 1977, and 4 October to 9 November, 1978. Bears were individually marked during these periods. Adult males, subadult males and subadult females were spatially segregated, the degree of segregation depending on density. Adult females and females with young were uncommon on the study area. Overall time budgets (i.e., active, inactive, social behavior) were similar for all age/sex classes, as were social behavior time budgets and social composition. There were few statistical differences in behavior between age/sex classes; adult males did spend more time in contact interaction, and contact interactions composed more of their total social behavior than for the other two age/sex classes. Adult male contact (social play) bouts were comprised of discrete motor acts. Social play between adult males was predictable and structured to some extent. The mutuality of initiator-receiver acts shows that two bouting bears respond to one another in a predictable manner. Bouts are structured in that there is a pronounced three-act dequence for both initiators and receivers, and most bouts have a vigorous "testing" phase. Initiators use aggressive acts more often and receivers use less aggressive, withdrawing acts more often. The aggregation of polar bears at certain locations during a non-competitive period in their annual cycle, with a concomitant increase in social behavior, is interpreted as a socializing process whereby individuals of this essentially solitary species may be able to better assess conspecifics at other times of the year when intraspecific competition is more intense. Social play was the most dynamic form of social behavior

observed in any age/sex class. In adult males, social play may enable assessment of strength and fighting capability of opponents. An individual may learn to associate its chances of success against conspecifics of different sizes that have certain strengths and fighting capabilities. Knowing when to escalate an altercation over an estrous female or a seal kill, and when not to, may be advantageous in avoiding serious injury from superior opponents.

ACKNOWLEDGEMENTS

Sincere thanks go to J. O. Murie, my supervisor, for his unending time, encouragement and advice throughout the course of this study. Special thanks go to I. Stirling, Canadian Wildlife Service, without whose support, advice and experience this study could not have been undertaken. I also wish to thank committee members D. M. Ross and B. Heming who offered useful criticism of this thesis, as did P. Smith. The cooperation and help of personnel from the Manitoba Department of Natural Resources both in Winnipeg and Churchill (Northern Resources Development Centre), especially R. Bukowsky and R. Goulden, is greatly appreciated. D. Andriashek and P. Smith provided invaluable field assistance in addition to good company during long periods of isolation at Cape Churchill. The aging of bear teeth was made possible through the laboratory assistance of W. Calvert. A. Wroot lent a helpful and patient ear during my early days of computer programming.

I am especially indebted to my parents, Bernard and Eleanor Latour, who have always encouraged my education and interest in biology.

This study was supported financially by the Canadian Wildlife Service, Edmonton, and the University of Alberta through a Graduate Teaching Assistantship and computing funds.

D. E. Zaiffdeen proficiently typed all drafts of this thesis.

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THESIS INTRODUCTION

The first European explorers and fur-traders recorded large numbers of polar bears along portions of the west coast of Hudson Bay during the ice-free season (July-November) (Tyrrell 1911, 1916; cited by Stirling et al. 1977). Adult males tend to concentrate at certain locations along the coast in the late summer and autumn while subadults and adult females move further inland. Because many of the bears gradually move northward during the summer and autumn, they accumulate at Cape Churchill, Manitoba, which appears to be the northern limit of their on-land movement (Stirling et al. 1977).

In 1977 and 1978, I arrived at Cape Churchill prior to the autumn accumulation of polar bears and remained there until the bears dispersed back onto the newly formed sea ice in November. My objective was to observe the social behavior of these temporarily concentrated, solitary carnivores. Several authors (Trautman 1963; Leyhausen 1965; Eisenberg 1967) have commented on the increased sociability, under certain circumstances, of solitary species. Since behavioral data exist for polar bears that are dispersed and actively hunting on arctic sea ice (Stirling 1974; Stirling and Latour 1978), it is possible to gain a comparative measure of the behavioral shift within a species between two extreme environmental conditions.

My data are presented in two papers:

1. Spatial relationships, time budget and interaction partners.
2. Analysis of the intense contact interaction between adult males.

The first paper deals with the spatial relationships between adult

males, subadult males and subadult females and the time budget and interaction partners for each of these three age/sex classes. The results are discussed, interpreted, and compared to other studies on aggregations of solitary carnivores, especially ursids. I discuss the behavior of the polar bears at Cape Churchill in light of the apparent lack of intraspecific competition on land, the shift in time budget toward greater sociability, and the flexibility of carnivore social systems (MacDonald 1977, 1979; Kruuk 1978).

All three age/sex classes were observed to participate in contact interactions or "bouts." Adult males, however, spent more time in contact interactions, and contact interactions composed the largest portion of all social interactions. In the second paper I examine these bouts between adult males. Possible functions of bouts are proposed based on theories of play and conflict and the behavioral ecology of polar bears.

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Paper 1

SPATIAL RELATIONSHIPS AND BEHAVIOR OF POLAR BEARS (*URSUS MARITIMUS* PHIPPS) CONCENTRATED ON LAND DURING THE ICE-FREE SEASON OF HUDSON BAY

ABSTRACT

I observed polar bears (*Ursus maritimus* Phipps) at Cape Churchill, Manitoba, a site where polar bears accumulate during the autumn when Hudson Bay is ice-free. Adult males, subadult males and subadult females were spatially segregated to a degree that depended primarily on density. Adult males showed the closest intra-class association. Subadult females spent more time in activity than did either adult or subadult males; this may be due to subadult females being approached more by other subadults. Much of an individual's social behavior occurred with members of its own age/sex class, perhaps a result of spatial segregation. In the non-competitive situation of this study, polar bears aggregated and were more social than when hunting on the sea ice. Increased sociability during this essentially "slack" period in their annual cycle may reinforce the social hierarchy, a factor important in the quick and non-injurious settlement of serious agonistic interactions at times of the year when competition is more intense. This study provides further evidence for the flexibility of carnivore social systems, not only between populations of the same species, but also within a single population.

INTRODUCTION

The Carnivora demonstrate a wide variety of social systems. These range from the complex social organization of certain felids and canids (e.g., Mech 1970; van Lawick and van Lawick-Goodall 1971; Kruuk 1972; Schaller 1972) to the flexible (but generally monogamous) system of other canids (e.g., Kleiman and Brady 1978) to what has been termed the "solitary" existence of some felid, mustelid and ursid species (e.g., Hornocker 1962; Eaton 1969; Eisenberg and Lockhart 1972; Rogers 1977; Craighead 1979; Powell 1979).

There exist few detailed behavioral ecology studies of the solitary species. Several studies have indicated that although individuals are solitary for much of the time outside of breeding periods, intense intraspecific interaction can occur, for example at prey carcasses. Such interactions over prey kills have been observed in tigers and bears (Schaller 1967; Stirling 1974; Craighead 1979).

Leyhausen (1965) gave the first detailed description of communal behavior in a solitary carnivore. He interpreted "social gatherings" of domestic cats in an urban surrounding as being important in familiarization and the continued societal organization of these animals. More recently, detailed studies of reproductive and social behavior indicate that selection mechanisms suspected in more social mammalian and avian species may also operate in solitary species (MacDonald 1977; Rogers 1977).

Excluding studies on captives, the most detailed work on social interactions of solitary species involves the concentration of individuals around a localized resource such as food (Hornocker 1962;

Stonorov and Stokes 1972; Egbert and Stokes 1976; Luque and Stokes 1976). Under these circumstances, a well defined social organization was maintained through simple, yet precise, agonistic signals.

The polar bear is a recently evolved predator of seals on ice-covered water (Erdbrink 1953). It is also opportunistic in that it scavenges both other bears' kills and carrion it happens upon during its regular movements (Stirling and Archibald 1977). The polar bear is circumpolar in distribution. In Canada it occurs over much of the Arctic Archipelago and south into Hudson and James Bays. Intensive mark-recapture studies in the High Arctic indicate that individuals restrict their movements to broadly defined home ranges measured in hundreds of square kilometres (Stirling et al. 1978). Strong evidence exists for a system of relatively isolated demes with occasional movement of individuals between them. The family group (i.e., a female with one or more young) is the only extended social unit. Polar bears are faced with an ice-free period during the warmer season, over much of their range. In arctic regions this time is spent widely dispersed along coastlines and, to a lesser extent, inland. However, in Hudson and James Bays, high densities occur on the mainland when the ice melts off these water bodies.

According to Stirling et al. (1977), polar bears remain on the pack-ice of Hudson Bay during December to July, hunting ringed seals (*Phoca hispida*), their main prey. Limited telemetry work and aerial track surveys indicated that the north-south oriented fracture zone approximately 5-100 km off the western shore is a preferred area. Mark-recapture studies suggest that the bears remain within Hudson Bay.

There is apparently little interchange between bears in Hudson Bay and those in adjacent regions such as Foxe Basin and James Bay. Breeding occurs on the pack-ice during April-May. The ice cover of Hudson Bay melts completely by early August and consequently the bears come ashore along the Manitoba and Ontario coasts.

Once ashore, a marked segregation of the population occurs. The majority of adult males remain close to the coast forming distinct aggregations at certain locations (Knudsen 1973; Stirling et al. 1977b). Females with young and pregnant females move 20-50 km inland. Immature males and females are generally found immediately inland from the coastal males.

As a result of the gradual northward movement along the coast of many of the bears, their numbers increase during September-November in the Cape Churchill region, the apparent northern limit of their on-land movement. Russell (1975) counted as many as 122 bears at Cape Churchill during aerial surveys in 1968-1970. In most years, immediately prior to freeze-up, it is not uncommon to see 50-80 bears on the narrow sandspit extending 2 km offshore from Cape Churchill. Polar bears also concentrate at several other locations along the Manitoba and Ontario coasts during late summer and fall (Knudsen 1973; Russell 1975). When freeze-up occurs, from early to late November, the bears rapidly disperse back onto the new sea ice.

The densities of polar bears concentrated at certain locations along the southwest coast of Hudson Bay are unique; although seasonal concentrations of polar bears have been reported elsewhere (Lutzyuk 1978), nowhere do densities approach those along Hudson Bay. The

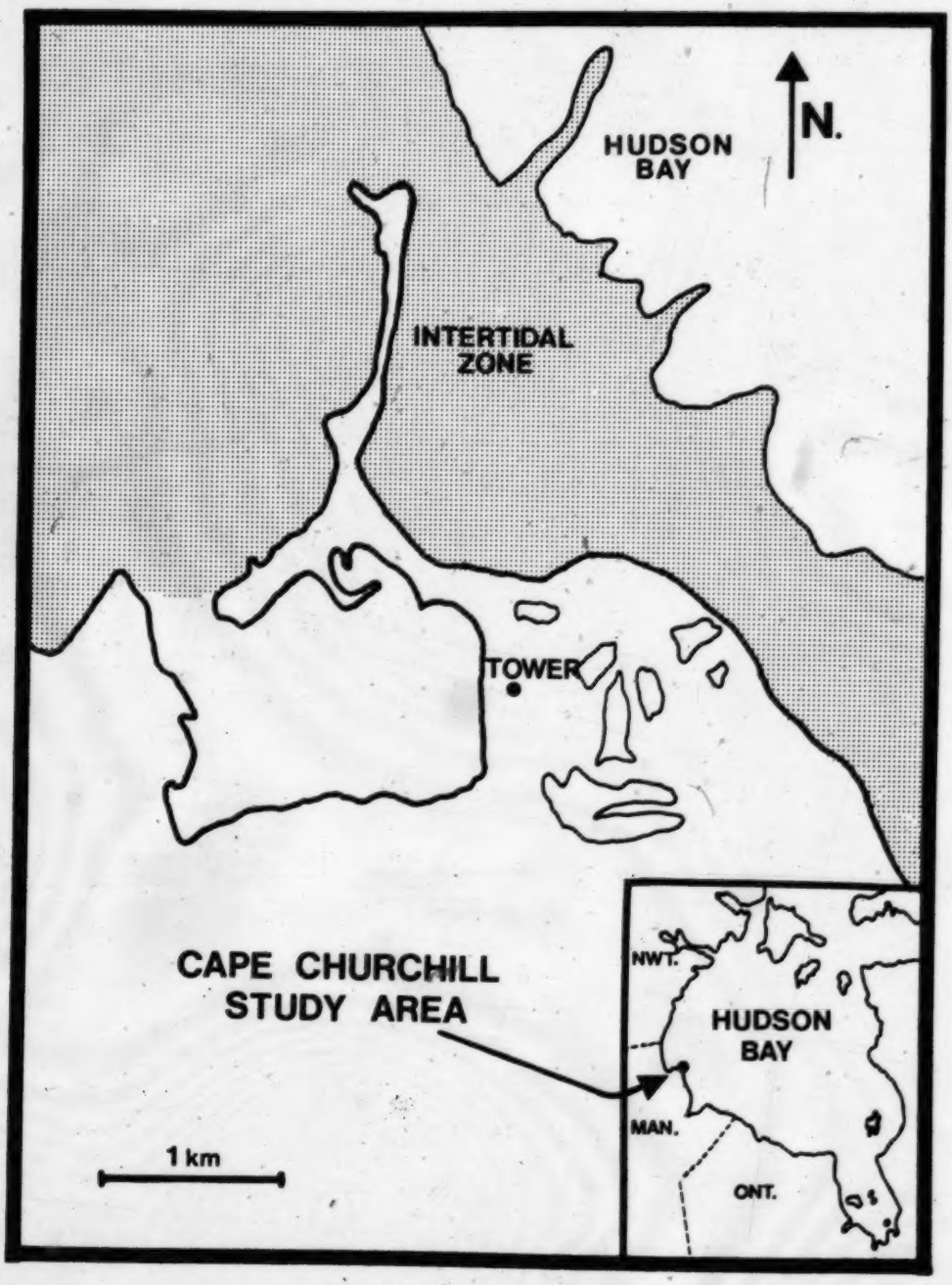
situation provides an exceptional opportunity to investigate the social organization and behavior of this solitary predatory species removed from its sea-ice habitat and in non-breeding condition.

In this paper I examine the spatial relationships between age/sex classes of polar bears aggregated at Cape Churchill, particularly the effects of density on spatial relationships and differences in intraclass association. I examine overall behavior by comparing time budgets of age/sex classes. Social behavior is addressed on both a time budget and a compositional basis. I discuss the results in light of other studies on concentrated carnivores, especially ursids. The seasonal shift in behavior is considered from the standpoint of differing ecological constraints and the flexibility of carnivore social systems.

STUDY AREA AND METHODS

The study area was located at Cape Churchill, Manitoba (58° 48' N, 93° 14' W) along the western shore of Hudson Bay. Cape Churchill lies in the coastal zone of the Hudson Bay Lowlands (Coombs 1954). Hustich (1957) described the area as subarctic. All my observations were confined to a 7 x 5 km area encompassing Cape Churchill. The east half of the area is composed of gravel beach ridges. Numerous fresh-water ponds and small lakes lie in the depressions between ridges (Fig. 1). Much of the west half of the study area is covered by a large, brackish lake which has contact with Hudson Bay during storm surges. Low, flat tundra extends south of the lake. All of these inland waters freeze over in mid-October. A 100 m wide sandspit extends 2 km northeast from the coast (Fig. 1). A broad intertidal zone consisting of boulder-strewn mudflats and sand

FIGURE 1. The Cape Churchill study area


HUDSON BAY
N.
INTERTIDAL ZONE
TOWER
CAPE CHURCHILL STUDY AREA
1 km
NWT.
HUDSON BAY
MAN.
ONT.

bars surrounds the sandspit. Vegetation on the study area reflects both arctic and more moist maritime conditions. Willow (*Salix* spp.), sedges (*Carex* spp.), mosses, lichens and arctic flowering plants are found in the moist depressions. Extensive stands of a tall, coarse grass (*Elymus* sp.) are found along the sandy ridges adjacent to the coastline.

All field observations were made from a 13.5 m tower on a gravel ridge 1.5 km southeast of the Cape Churchill sandspit (Fig. 1). The observation hut supported by the tower also served as permanent living quarters. My assistant and I arrived at the tower prior to the annual autumn accumulation of polar bears and remained there until the mid-November freeze-up of Hudson Bay. Observations were made during the following periods: 1977 - 12 Sept-3 Oct and 10 Oct-19 Nov; 1978 - 3 Oct-9 Nov. Data were collected daily (approx. 0830-1700) except on occasions when bad weather reduced visibility.

Capture and individual marking of polar bears continued during the study period. Some bears were captured using cable foot snares at baited sites immediately around the tower (Jonkel 1967) and were subsequently immobilized with darts containing tranquilizers (Lentfer 1968). Free-ranging bears were also darted from the tower. In 1977, a helicopter was used to capture bears prior to the first observation period and midway through the second observation period (see Fig. 2 for period times). Each bear was permanently marked with delrin ear tags and a number tatooed inside the upper lip. These markings enabled identification of the individual during this and other studies of polar bears in Manitoba. A large, black number was painted with permanent fur dye (Nyanzol) on both sides of the mid-section. Bears marked in this

manner could be identified from 3 km with the aid of a spotting scope. The bear's weight was estimated using a cattle girth tape (Stirling et al. 1977). A pre-molar was extracted for later age determination using the thin section methods described by Stirling et al. (1978). Straight-line length, shoulder height (wrist to top of shoulder hump) and chest girth were recorded. Behavioral data were not collected on bears for 3 days subsequent to their capture.

To obtain data on spatial relationships and approximate densities of bears present on the study area, a 360° scan of the study area was made each day at sunrise, midday and sunset. The locations of all marked and unmarked bears were plotted on a map using local topographic features to obtain a position. The resolving power of this technique was about 50 m. Unmarked bears were identified as adult male, subadult, female with young or, if they were too distant or partially hidden, as unclassified. Adult males were readily distinguishable by their large size (Table 1) and distinct body profile. Subadults were generally recognizable by their small size and profile, but sex could not be determined at a distance. Females accompanied by young were readily distinguishable, but were not common on the study area. Lone adult females were also rare on the study area (only 2 of 72 captured adults and subadults were lone adult females). For spatial analysis, all marked and unmarked subadults were pooled into one category, because of the much greater proportion of unmarked to marked bears and, therefore, the often closer proximity of unmarked subadults. For each adult male and subadult identified during a scan period, the following distances were obtained directly from the location map for that scan period:

TABLE 1

Polar bear capture data for both years

Bear category	No. of bears captured		Mean age (yr) and SE		Mean weight (kg) and SE	
	1977	1978	1977	1978	1977	1978
Ad ♂♂	14	10	9.4±2.7	9.3±1.0	345±18	345±18
Subad ♂♂	18	13	2.7±0.3	2.5±0.3	177±11	184±14
Subad ♀♀	7	8	2.3±0.3	2.8±0.2	125±10	137± 9

adult male to nearest adult male, adult male to nearest subadult, subadult to nearest adult male, and subadult to nearest subadult.

Polar bears within 300 m of the observation tower could be observed unaided. Distant bears were observed with a 15-60X Bausch and Lomb spotting scope. As many marked bears as possible were located at the beginning of each day; then, depending on the number located, each observer chose two or three bears and initiated a separate continuous behavior record on each (focal animal technique, Altmann 1974). Usually only 5-8 marked bears were located at daybreak so behavior records were commonly initiated on them all. Because bears were inactive much of the time it was not difficult to record the behavior of more than one individual, nor was there great loss of detail. The flat, treeless terrain generally permitted uninterrupted viewing except for short disappearances behind ridges or in thick shrubbery. A focal bear's record was terminated only when it walked too far away for detailed observation, or occasionally when visibility was reduced by fog or blowing snow. If a focal bear disappeared behind a ridge or in vegetation, and reappeared nearby later, it was assumed to have been lying down during that time. The topography of the study area was such that a bear standing, and therefore active, was almost always partially visible.

A focal individual's behavior was recorded by noting the time to the nearest minute of all behavior changes. In addition, other details such as location, presence of vegetation, direction of movement, and proximity of other bears were recorded. When a social interaction occurred the identity of the conspecific was recorded or, if it was an

unmarked bear, described as either adult male, subadult or unclassified. Non-social behavior was classified as walking, standing, sitting, lying or feeding. For analysis, all behaviors except lying were pooled under the broader category of active behavior; lying was considered inactive behavior. Social behavior was classified as follows:

Contact - The focal bear approaches another (or vice versa), or they both approach and there is physical contact, usually naso-nasal. The interaction may escalate to a more vigorous "bout" or the two bears may move apart.

Avoids - The focal bear shows obvious moving away from another bear.

Is Avoided - Another bear shows obvious moving away from the focal bear.

Approaches - The focal bear moves toward another bear.

Is Approached - Another bear moves toward the focal bear.

Awareness - The focal bear obviously perceives the presence of another bear by looking toward it intently; the other bear may or may not acknowledge the presence of the focal bear.

Follow - The focal bear walks along behind another bear, usually no more than 100 m apart.

In the time budget analysis all marked bears were classified as adult male, subadult male or subadult female. Individuals 5 years and younger were classified as subadults while males 6 years and older were

classified as adults. This dichotomy was based on histological and population ecology studies of brown and polar bears which place male-female sexual maturity at 4-5 years (Erickson et al. 1968; Pearson 1975; Stirling et al. 1978).

The 1977 and 1978 study periods were each divided into three periods of equal length (Fig. 2), the limits of which did not correspond to any particular phenological events during the study period. These periods served as discrete units, free of conscious bias, by which possible density effects on bear behavior over time could be analysed.

Estimates of the rate of bear influx onto the study area were obtained by calculating regression coefficients (slopes) from census data for the periods within each year. I used non-parametric statistics for the remaining analyses (Siegel 1956; Marascuilo and McSweeney 1977). A probability value less than .05 was considered significant unless otherwise stated. Further details of the analysis are supplied where appropriate.

RESULTS

A. Relative Densities

Figure 2 is a graphical presentation of census data throughout the 1977 and 1978 study periods; the daily mean for every second day is plotted. Data are missing for the last several days of the 1978 study period primarily because of bad weather. Table 2 provides numerical information useful in the interpretation of Figure 2. I had no reason to believe that the ratio of adult males to subadults in the unclassified category (Table 2) differed from the ratio of marked adults to subadults.

FIGURE 2. Mean counts of polar bears for every second day of each observation season

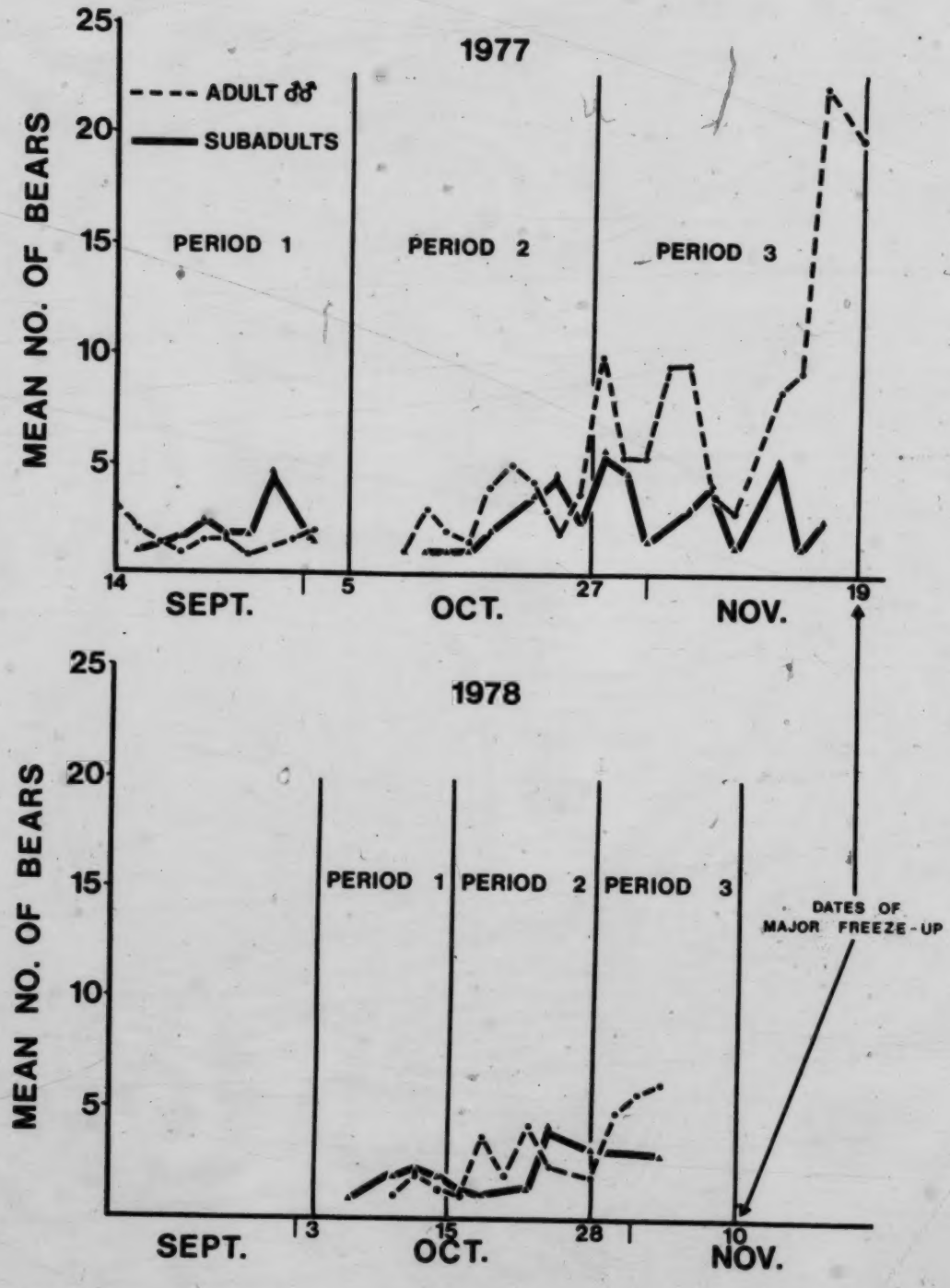

1977
ADULT ♂♂
SUBADULTS
MEAN NO. OF BEARS
25
20
15
10
5
PERIOD 1
PERIOD 2
PERIOD 3
14
SEPT.
5
OCT.
27
NOV.
19
1978
MEAN NO. OF BEARS
PERIOD 1
PERIOD 2
PERIOD 3
DATES OF MAJOR FREEZE-UP
3
SEPT.
15
OCT.
28
10
NOV.

TABLE 2

Census, rate of increase and ratio data for all adult ♂♂ and subadults in both observation seasons

Year	Period	Average number of bears per count and rate of increase					Ratio of Ad ♂♂:Subadults:Unclassified		
		Ad ♂♂	Regression coefficient	Sub-adults	Regression coefficient	Unclassified	Ad ♂♂	Sub-adults	Unclassified
1977	1	.90	-.05	2.38	.05	2.38	.38	1.00	2.64
	2	3.09	.20	2.31	.23	4.13	1.34	1.00	1.79
	3	7.75	.22	3.59	-.12	5.20	2.16	1.00	1.45
1978	1	.73	.20	1.82	.06	2.36	.40	1.00	3.25
	2	1.93	-.01	1.52	.23	2.24	1.27	1.00	1.47
	3	4.89	.02	1.67	.03	3.94	2.93	1.00	2.36

Therefore, I assume that the ratios of adult males to subadults (Table 2) are accurate estimates of true ratios.

Approximately twice the number of adult males and subadults were on the study area in 1977 compared to 1978. In period 1 of both years subadults were more than twice as abundant as adult males; the ratio shifted in slight favor of adult males during period 2. Period 3 of both years was characterized by a continued increase of adult males. The regression coefficients (slopes) of Table 2 indicate the gradual build-up of both adult males and subadults in 1977 and 1978. Comparisons between 1978 and the corresponding time span in 1977 show similar ratios of adult males to subadults (1.52:1.00 in 1977 and 1.40:1.00 in 1978). Similarly, rates of increase differed little (.16 and .03 in 1977 and .14 and .03 in 1978). Comparison between 1978 and the entire 1977 study period indicates similar ratios and rates of increase (1.45:1.00 in 1977 and 1.40:1.00 in 1978; .13 and .03 in 1977 and .14 and .03 in 1978). The low overall regression coefficients of .03 for subadults in both years represents the build-up of subadults at the beginning, levelling off, then a slight decline in period 3 (Fig. 2).

Not all bears that arrived on the study area stayed until freeze-up. Therefore the census data presented here serve to indicate only numbers of bears present at a particular time and not changes to a group of bears always present on the study area. From September through early October the bear population on the study area was relatively constant. Later on, however, movement through the study area became more common. In 1977, the proportion of bears that were resighted more than one week after being marked was 80% of 14 in period 1, 65% of 18 in period 2, and 57% of 7 in period 3. In 1978, the respective values were 60% of 5,

53% of 15, and 14% of 14. Resight information provided to me by other researchers indicates that 40-50% of the subadults marked on the study area moved 60 km west to the vicinity of Churchill townsite. By contrast, in 1977 only 1 of 14 marked adult males, and in 1978 only 1 of 10, were resighted in the Churchill area.

B. Distribution and Association

Approximately one-half of the rectangular study area is either sea or intertidal zone. If only the mainland portion of the study area is considered (including the long sandspit), the distribution of marked adult males, subadult males and subadult females was highly clumped (χ^2 Goodness of fit test, $P < 0.001$). This was true for both the entire 1977 and 1978 study periods and the three observation periods for each year.

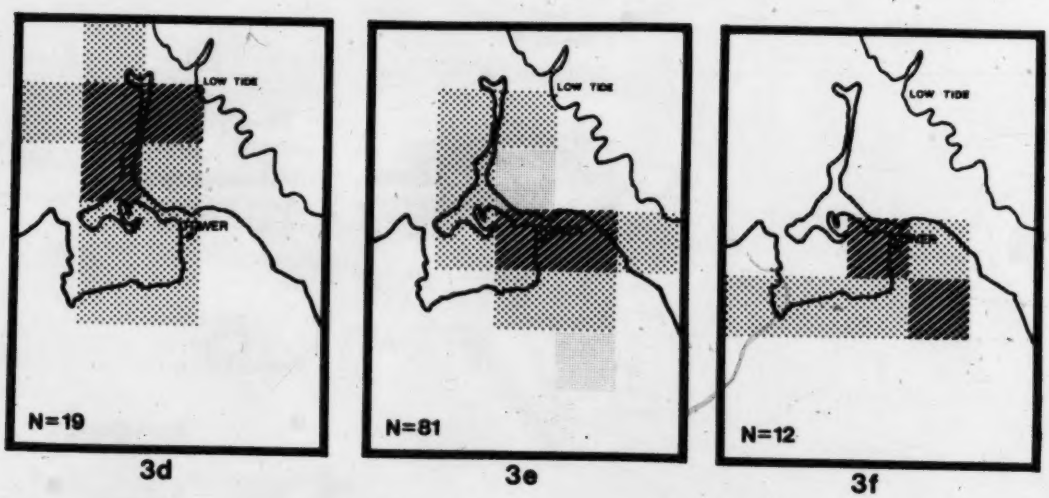
Figure 3 is a pictorial representation of the distribution patterns for 1977 and 1978. The 200 m x 200 m cells into which the study area was divided were consolidated into 1 km^2 units and the proportions of sightings for marked adult males, subadult males and subadult females in each unit were calculated. In both years, the sandspit northwest of the observation tower was a major concentration area for adult males; subadult males concentrated on the mainland area immediately to the south. However, at the higher density conditions in 1977, adult males overlapped considerably with subadult males south of the sandspit. The subadult female pattern was similar for both years; they were seen most on the periphery of the area occupied by adult males - subadult males (1977) and subadult males (1978). Subadult females were sighted occasionally on the sandspit in 1977 but not in 1978.

FIGURE 3. Percentage of marked adult males (3a), subadult males (3b) and subadult females (3c) sighted in each 1 km^2 unit in 1977, and in 1978 (3d-3f)
(N = total number of sightings of marked bears)

1977

3a 3b 3c

1978



3d 3e 3f

-≤1% -2-10% -11-60%

Table 3 presents spacing data obtained by converting the measurement between plotted bear locations to true distance. Distance between adult males decreased significantly over the three periods in both 1977 and 1978 (Kruskal-Wallis test, $P < 0.05$). Adult male to subadult distance was greater during period 2 in both years, but only in 1977 was this difference significant ($P < 0.05$). In 1977, subadult to adult distance was similar during periods 1-2, then decreased significantly during period 3 ($P < 0.05$), whereas in 1978 there was no significant change across all three periods. Distance between subadults decreased significantly ($P < 0.05$) between periods 1-2 in 1977 but showed no significant change in 1978 across periods 1-3.

Adult males were located closer to one another in both 1977 and 1978 than they were to subadults or subadults to them (Table 4). In 1977, adult male to subadult distance was significantly greater than subadult to adult male distance (mean distance of 1,655 m and 1,365 m respectively). In contrast, there was no significance between these two distance categories in 1978 (mean distances of 1,690 m and 1,698 m respectively). The second difference between years occurred between subadult to adult male and subadult to subadult distances; in 1978 subadults were significantly closer to one another than they were to adult males, whereas in 1977 these distances did not differ significantly.

C. Time Budget and Social Behavior Analysis

Time budget data is based on 2,419 hours of observation over the two-season study (Table 5). Data were not obtained on all marked bears because of the transiency of some bears on the study area. The total

TABLE 3

Distances between bear classes and results of Kruskal-Wallis one-way analysis of variance comparisons between periods (S - significant difference, NS - no significant difference)

Year	Bear→bear distance category	N	Mean (m) and SE of measurements for 1977 and 1978		Mean (m) and SE of measurements for each period in 1977 and 1978									χ^2 significance for 3 period comparison (α = .05)
					Period 1			Period 2			Period 3			
			Mean (m)	SE (m)	N	Mean (m)	SE (m)	N	Mean (m)	SE (m)	N	Mean (m)	SE (m)	
1977	Ad ♂♂→Ad ♂♂	95	773	94	11	1737	475	30	801	172	54	558	77	S
	Ad ♂♂→Subad	95	1655	84	20	1466	146	24	2345	155	51	1400	96	S
	Subad→Ad ♂♂	97	1365	81	24	1850	148	21	1689	218	52	1011	91	S
	Subad→Subad	97	1084	85	39	1436	120	21	751	148	37	903	144	S
1978	Ad ♂♂→Ad ♂♂	37	647	125	3	2667	136	16	554	107	18	411	124	S
	Ad ♂♂→Subad	37	1690	170	6	1092	460	19	1907	165	12	1664	413	NS
	Subad→Ad ♂♂	36	1698	164	6	1358	397	18	1810	219	11	1702	340	NS
	Subad→Subad	36	737	98	11	818	210	14	550	82	8	955	266	NS

TABLE 4

Results of Kolmogorov-Smirnov two sample test comparisons between distance categories within each year

TWO DISTANCE CATEGORIES BEING COMPARED						SIGNIFICANCE (α =0.05) 1977	SIGNIFICANCE (α =0.05) 1978
	N(1977)	N(1978)		N(1977)	N(1978)		
Ad ♂♂ → Ad ♂♂	95	37	Ad ♂♂ → Subad	95	37	S	S
Ad ♂♂ → Ad ♂♂	95	37	Subad → Ad ♂♂	97	36	S	S
Ad ♂♂ → Ad ♂♂	95	37	Subad → Subad	97	36	S	S
Ad ♂♂ → Subad	95	37	Subad → Ad ♂♂	97	36	S	NS
Ad ♂♂ → Subad	95	37	Subad → Subad	97	36	S	S
Subad → Ad ♂♂	97	36	Subad → Subad	97	36	NS	S

observation time for individuals varied considerably: adult males - 3 h to 50 h, subadult males - 6 h to 170 h, subadult females - 4 h to 91 h. The high standard errors for all categories of behavior indicate considerable individual variability.

Significant differences in activity between age/sex classes occurred in 1978 only. Subadult females spent significantly less time inactive than either adult or subadult males (Kruskal-Wallis test, $P < 0.05$). In 1977, the same trend was evident but the differences were not significant. When the data from both years were pooled subadult females differed from adult and subadult males in both active and inactive behavior.

The various social behaviors form such small proportions of total observation time that I pooled them under the broader category of social behavior (Table 5). In both years there were no significant differences in time spent in social behavior time between any of the three age/sex classes.

Pairwise comparisons for the three age/sex classes between years showed no significant differences in active, inactive or social behavior.

To investigate whether time spent in the various types of social behavior differed for the three age/sex classes, the proportions (%) that each interaction type contributed to total social behavior time were calculated (Table 6). Once again, high standard error values indicate considerable individual variability. There was also much variability within age/sex classes between years. For example, subadult females varied from 0% to 23.2% for contact behavior between 1977 and 1978.

TABLE 5

Mean percent of total observation time and Kruskal-Wallis Anova comparisons between age/sex classes (S - significant, NS - non-significant)

Year	Bear category	Hours of observation	N	Active			Inactive			Social behavior		
				Mean	SE	α=0.05	Mean	SE	α=0.05	Mean	SE	α=0.05
1977	Ad ♂♂	318.8	8	17.3%	3.6%		79.4%	6.3%		3.0%	1.4%	
	Subad ♂♂	1106.0	17	20.4%	2.5%	NS	75.1%	3.5%	NS	4.3%	1.4%	NS
	Subad ♀♀	350.2	6	36.9%	12.6%		59.2%	13.8%		3.3%	1.6%	
1978	Ad ♂♂	115.9	4	19.9%	5.3%		76.8%	4.4%		3.1%	1.5%	
	Subad ♂♂	395.3	11	27.2%	6.9%	NS	70.2%	6.9%	S	2.8%	.6%	NS
	Subad ♀♀	132.7	5	35.4%	3.4%		52.8%	7.1%		12.8%	6.1%	
Pooled	Ad ♂♂	434.7	12	18.0%	2.9%		78.6%	4.3%		3.1%	1.5%	
	Subad ♂♂	1501.3	28	22.8%	3.0%	S	73.2%	3.4%	S	3.8%	1.9%	NS
	Subad ♀♀	482.9	11	36.5%	6.7%		56.3%	7.9%		7.6%	3.5%	

TABLE 6

Social behavior time budget for each age/sex class

Year	Bear category	N	Mean Proportions of Total Amount of Time Spent in Social Interaction													
			Contact		Approaches		Is Approached		Avoids		Is Avoided		Awareness		Follow	
			Mean(%)	SE	Mean(%)	SE	Mean(%)	SE	Mean(%)	SE	Mean(%)	SE	Mean(%)	SE	Mean(%)	SE
1977	Ad ♂♂	8	29.9	9.7	8.2	4.7	.5	.5	8.8	5.7	5.8	2.7	21.8	8.0	0.0	0.0
	Subad ♂♂	17	26.3	7.4	10.5	3.6	11.0	5.4	17.3	6.3	1.3	.8	21.1	5.6	.7	.4
	Subad ♀♀	6	0.0	0.0	7.6	7.1	5.1	5.1	21.2	9.0	.7	.7	48.8	16.8	0.0	0.0
1978	Ad ♂♂	4	47.6	19.2	2.2	2.2	.6	.6	0.0	0.0	.6	.6	21.8	15.2	2.7	1.8
	Subad ♂♂	11	6.0	4.9	4.0	1.8	20.2	5.5	.4	.4	0.0	0.0	51.1	6.8	9.3	6.2
	Subad ♀♀	5	23.2	14.1	11.6	5.8	36.2	17.2	.7	.7	.1	.1	23.6	9.9	4.6	3.0
Pooled 1977 & 1978	Ad ♂♂	12	35.8	9.0	6.2	3.2	.5	.4	5.9	3.9	4.1	1.9	21.7	7.0	.8	.6
	Subad ♂♂	28	18.3	5.2	7.9	2.4	14.6	4.0	10.7	4.0	.8	.5	32.9	5.1	4.1	2.5
	Subad ♀♀	11	10.6	7.0	9.4	4.5	19.2	9.2	11.9	5.7	.4	.4	37.3	10.5	2.1	1.5

Adult males showed the most contact interaction in both years. However, when data from 1977 and 1978 were pooled, no significant differences in social behavior time were obtained between the three age/sex classes.

I did not attempt a frequency analysis of social behavior in this study. As Altmann and Altmann (1977) state, the exact make-up of a stable population must be known before one can proceed with frequency analysis. I have only estimates of relative age/sex class abundance (Table 2) and, as pointed out earlier, the population of bears on the study area was not stable. However, composition of social behavior was analysed using the proportion of total number of interactions for the three age/sex classes (Table 7). Comparisons by chi-square were made between the three age/sex classes using arcsine transformed proportions (Marascuilo and McSweeney 1977). No significant differences were obtained between the three classes for any of the seven social behavior categories. Contact, however, neared significance ($P < 0.1$), with adult males having the highest proportion and subadult females the lowest. Similarly, the "Is Approached" category neared significance ($P < 0.1$); subadult females had the highest proportion and adult males the lowest.

D. Interaction Partners

This section deals with the class of bear that individuals within each of the three age/sex classes interacted with. Although insufficient data (i.e., $N < 6$ interactions) precluded a complete analysis, certain trends were apparent.

TABLE 7

Composition of social behavior based on total number of interactions for each age/sex class

Bear category	N	Total observation time (hr)	Total no. of interactions	Proportion, Number, Mean (min) and SE of all Social Interactions (1977 and 1978 Pooled)											
				Contact		Approaches		Is Approached		Avoids		Is Avoided		Awareness		Follow	
				Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
Ad ♂♂	12	434.7	97	.36	35	.14	14	.02	2	.06	6	.11	11	.26	25	.04	4
Subad ♂♂	28	1501.3	309	.24	73	.10	30	.13	39	.12	36	.04	13	.35	108	.03	10
Subad ♀♀	11	482.9	121	.19	23	.15	18	.21	25	.06	7	.02	2	.31	37	.07	8

Contact. For adult males, subadult males and subadult females, 100% of all contact interactions were initiated with individuals of the same class (N = 35, 73 and 23 respectively).

Approaches - Is Approached. In order to increase the sample size for "Approaches - Is Approached" I pooled subadult males and females. Adult males approached other adult males significantly more often than they approached subadults ($\chi^2 = 7.12$, $P < .01$, $N = 17$). Insufficient data on adult males prevented comparisons for "Is Approached" behavior. Subadults approached other subadults more often than they did adult males ($\chi^2 = 5.54$, $P < 0.05$, $N = 26$). Conversely, subadults were not approached by any one age/sex class more than another.

Avoids - Is Avoided. Data on "Avoids" and "Is Avoided" behavior were insufficient for both adult males and subadult females. Subadult males did not avoid any one age/sex class more than another. Subadult males were avoided by other subadults more often than they were by adult males ($\chi^2 = 8.0$, $P < 0.01$, $N = 8$).

Awareness. Adult males were significantly more aware of other adult males than of subadults ($\chi^2 = 13.5$, $P < 0.001$, $N = 24$). Subadult males and females did not show significant differences in awareness.

Follow. Data on all three age/sex classes were insufficient for analysis.

DISCUSSION

The degree of age/sex class segregation of polar bears on the study area is directly related to density as shown by between season similarities and differences. For example, in both years adult male to subadult distance was greater in observation period 2 than in either period 1 or 3. This was related to the influx of adult males onto the study area and their accumulation, primarily on the sandspit, during the latter half of observation period 2 (Fig. 2). This resulted in a marked segregation of adult males and subadults during the latter half of period 2; however, as more adult males arrived during observation period 3 (Fig. 2), adult males and subadults associated more closely, primarily in the area immediately south of the sandspit (Fig. 3). In the higher density year of 1977, distance between subadults and adult males decreased in period 3 and was similar to the distance between subadults. In contrast, the lower density year of 1978 had more pronounced age/sex class segregation as indicated by Figures 3d-3f, and the similarity of distances between adult males and subadults and between subadults and adult males (Table 4). These between year differences indicate greater age/sex class association at higher density rather than accommodation through "spreading out."

The density differences between 1977 and 1978 did not result in marked differences in the behavior of the bears between years. Overall time budgets (Table 5) and social time budgets (Table 6) were similar for all age/sex classes when data were pooled for both years. Subadult females did spend significantly more time actively and less time inactively than did adult or subadult males. That subadult

females were "Approached" more often than adult or subadult males may account for their higher active time, since the approach of another bear usually elicited movement.

Social composition was similar for all three age/sex classes, although contact behavior was highest for adult males. The bears tended to interact with members of their own class. In particular, contact behavior involved partners of the same age/sex class. Both forms of approach behavior involved similar age/sex class individuals, and subadult males both avoided and were avoided by other subadult males most.

My data suggest a system of general age/sex class segregation characterized by varying degrees of association between age/sex classes, depending primarily on density. This system appears similar to that found in girzzly bears (Hornocker 1962; Egbert and Stokes 1976) and black bears (Rogers 1977) as well as that seen in other non-breeding aggregations of mammals (Harestad and Fisher 1975; Miller 1976). Indeed, as Christian (1970) points out, social organization based on hierarchies of social rank between individuals, families or coherent groups is an almost universal mammalian feature. Segregation in the above studies was maintained by both passive avoidance and direct agonistic interaction, and in these contexts certain inter-class dominance relationships were established. For the polar bears in this study, the mechanisms of segregation were more subtle, and segregation was probably more a result of a continuous avoidance of conspecifics rather than through overt acts of approach and avoidance.

The spatial and behavioral relationships of the bears at Cape Churchill indicate a degree of internal organization suggestive of an

aggregation as defined by Eisenberg (1966, p. 1), "If an animal has some degree of tolerance for conspecifics it may form temporary aggregations which show only limited coordination and integration." Knudsen (1973) concluded that the numbers and sizes of the polar bear aggregations which occur at several traditional locations along the west coast of Hudson Bay were greater than could be explained by chance alone. Various reasons for their existence have been suggested (e.g., insects, temperature, proximity to first ice formation) but none are compelling in light of actual conditions during a typical autumn. What advantage could polar bears gain by aggregating at certain locations given the approximately 600 km of coastline along which the population of 1,800-2,000 bears (Stirling, pers. comm.) could disperse? Might not individuals of this "solitary" species be expected to spend the ice-free season inactively, dispersed randomly along the coast, and ignoring conspecifics. Intuitively, this would seem to be the best tactic for minimizing interaction (especially agonistic) between individuals of this essentially solitary species.

All indications are that the polar bears at Cape Churchill are not competing for resources such as food, mates and space. They are temporarily removed from their specialized predatory niche. My data and Knudsen's (1978) for a similar situation on North Twin Island in James Bay show that they spend little time feeding (1.25% and 3.4% respectively). Russell (1975) recorded a variety of food items consumed by these bears (i.e., coarse grasses, carrion, kelp) but he had no measure of ingestion rates or caloric value. Breeding occurs during April-May and adult females were observed only occasionally on the study

area. Perhaps the bears in this study are using this essentially slack, non-competitive time in their annual cycle as a socialization period. Stirling (1974, pers. comm.) states that the hunting bears in his summer study spent considerably less than 2% of total observation time in any form of social behavior. In the present study, depending on age/sex class, 3-8% of time was spent in social behavior. Through aggregation and heightened sociability an individual may be able to better assess its position in a social hierarchy. Such knowledge could be advantageous in the quick and non-injurious settlement of future disputes over kills or mates. Stirling (1974) describes several instances of intraspecific competition observed around seal kills. In addition, there is also intense competition during the 6-8 week breeding period in late winter-early spring. I have witnessed agonistic encounters between adult males attempting to gain access to estrous females in the High Arctic. Frontal wounding of adult males during this period in adult males provides evidence for the intensity of these interactions.

Wilson (1975) proposed that animals in a "temporarily generous environment" will shift their time budget from priority activities such as foraging, antipredation and reproduction to non-foraging, low priority activities. He defines a generous environment as having an abundance of food. Despite the absence of abundant food, the principle of time allocation may apply to the bear aggregation at Cape Churchill. In the complete absence of priority activities such as foraging, antipredation or reproduction, the situation is essentially as, or more non-competitive than exists when food is "superabundant." Shifting the time budget under non-competitive conditions allows for the increased socialization reported in this study.

Although caution is required (Fisler 1967), comparison of my data with that obtained for more social species illustrates the behavioral shift between solitary and aggregated polar bears. Fisler points out that time budgeting of social behavior may not necessarily be indicative of importance, and measures such as frequency may be more important. Also, in comparing social species with less social species, the influence of long-term association on social relationships should be considered. Nonetheless, when aggregated on land, polar bears spend as much time interacting as many more social species. For example, primates spend .4-8% of their time in social behavior, depending on species (Fisler 1967; Clutton-Brock 1974; Pinto et al. 1974; Slatkin and Hausfater 1976; Wright 1978); ungulates are seasonally variable but values of 1-15% are the rule (Spinage 1968; Guy 1976; Berger 1977). The avian literature indicates values of 2-9% for breeding males of several species (Verner 1965; Schartz and Zimmerman 1971; Dwyer 1975).

Recently MacDonald (1977, 1979) and Kruuk (1978) introduced the concept of intraspecific flexibility in carnivore social systems. To date, however, fixed differences between two or more intraspecific groups have been the main consideration. More recently, Bekoff and Wells (1980) considered annual behavior changes within a single group. My study is concerned with a species undergoing annual changes in behavior, from actively hunting, essentially solitary individuals to aggregations of non-hunting individuals. The above authors attempted to relate social system flexibility to resource location, quality and quantity (e.g., food). In my study, all factors usually considered as primary resources were lacking. Under non-competitive conditions a

population of solitary carnivores can reallocate their total active time toward more social behavior. That competition directly affects amount and type of social interaction was shown by Egbert and Stokes (1976), who reported serious aggressive encounters and much avoidance between brown bears competing for salmon along a river. When salmon increased, thereby reducing competition, there was a concomitant decrease in aggression and an increase in amicable behavior such as play.

Leyhausen (1965) and Eisenberg (1967) were among the first to recognize the adjustable social systems of some so-called solitary species that oscillate between dispersed solitary and more tolerant, semi-communal individuals, depending upon environmental conditions and population density. Social plasticity characterizes the Ursidae (Rogers 1977; Craighead 1979). Usually solitary individuals can aggregate either as a result of attraction to something of common benefit or, as I discuss in this paper, an elevated sociability between individuals when inter-individual competition is at a minimum. Greater sociability at these times may increase the precision of social relationships, an important consideration at other times when intraspecific competition is more intense.

ACKNOWLEDGEMENTS

This study was supported financially by the Canadian Wildlife Service, Edmonton, and the University of Alberta. Special thanks go to J. O. Murie, University of Alberta, and I. Stirling, Canadian Wildlife Service, for their continued support, advice, and criticism during this study. The cooperation and help of the Manitoba Department of Natural Resources, especially R. Bukowsky and R. Goulden, is greatly appreciated. D. M. Ross and B. Heming, University of Alberta, provided useful criticism of an earlier draft, as did P. Smith. The field assistance of D. Andriashek and P. Smith contributed in large measure to the success of this work.

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Paper 2

INTERACTIONS BETWEEN FREE-RANGING, ADULT MALE POLAR BEARS (*URSUS MARITIMUS* PHIPPS): A CASE OF ADULT SOCIAL PLAY

ABSTRACT

I observed 73 dyadic interactions (bouts) between adult male polar bears (> 6 years) at Cape Churchill, Manitoba, from 4 October to 9 November, 1978. All bouts involved at least one marked bear. I classified these bouts as social play and in this paper I discuss the criteria used for this classification. Social play bouts were comprised of discrete motor acts and showed some predictability and structure. Two bouting bears respond to one another in a predictable manner as indicated by the mutuality of initiator-receiver acts. Structuring was suggested by a major three-act sequence for both initiators and receivers. Aggressive acts were found to be characteristic of initiators; the less aggressive, withdrawing acts were characteristic of receivers. The results are interpreted from both the structuralist and functionalist approaches to social play. I hypothesize that social play between adult male polar bears during the non-competitive period of their annual cycle serves as a socialization process facilitating both opponent assessment and the refinement of social interaction. Both of these are probably important at times of the year when intraspecific competition is more intense.

INTRODUCTION

Polar bears come ashore along the west coast of Hudson Bay from mid to late summer when the pack ice melts (late June to late July). Pregnant females and those with young move inland, while adult males and subadults of both sexes generally remain near the coast. The bears feed very little during this time on land (Latour 1980). Marked aggregations of bears occur at certain locations along the coast (Knudsen 1973; Stirling et al. 1977a). Latour (1980) discussed spatial relationships and time budgets for bears at one of these traditional aggregation sites. The time spent in different behaviors was similar for all age/sex classes. Social behavior comprised 3-8% of total time depending on age/sex class. Social behavior was of several types; contact behavior formed the second largest proportion (approx. 22%, depending on age/sex class) after awareness. Adult males spent a larger proportion of their total number of social encounters in contact behavior than did subadult classes. Adult males also showed the strongest tendency to aggregate.

This paper describes contact bouts between adult males. Particular attention is paid to bout structure, initiator-receiver differences, and variability between bouts. Bouting is discussed in light of current concepts of play behavior and animal conflict (e.g., Fagen 1974, 1977; Parker 1974; Bekoff 1975; Maynard Smith and Parker 1976).

METHODS

This study was done at Cape Churchill, Manitoba (58° 46' N, 93° 14' W) on the coastal, subarctic tundra of Hudson Bay (Latour 1980). Observations were made from a 13.5 m tower constructed 1.5 km southeast of the Cape Churchill sandspit. Polar bears were captured and individually marked throughout the study period (Latour 1980). Data reported here were collected from 3 October to 9 November 1978.

Contact behavior refers to any instance of physical contact between individuals. Initial contact commonly escalated to prolonged interaction involving distinct acts; herein, these interactions are referred to as bouts. I use bout in the sense of Lehner's (1979) type 2 definition of bout as "a relatively stereotyped sequence of behaviors that occur in a burst."

All bouts reported here involved two adult males of which one was always marked. Latour (1980) outlined the criteria used to differentiate adults from subadults. The study area was kept under constant surveillance, and I recorded as many bouts as possible using a keyboard that activated a 20 pen event recorder. Bouts within 300 m of the tower could be observed unaided, but those farther away (maximum distance = 1.5 km) required use of a 15-60X spotting scope. Bouts were described using a set of 14 distinct acts obtained from preliminary observation during the preceding autumn. The first 10 keys were used for the initiator of the bout and the last 10 for the receiver. The 14 acts for initiator and receiver were accommodated on the 20 pen event recorder by activating two keys simultaneously for certain acts. The initiator of a bout was the individual that approached the other (receiver) and

instigated first contact. All bouts had one obvious initiator. Recording commenced when first contact was made and terminated when one or both bears withdrew and did not reunite within 30 sec, or when the two faced each other for more than 30 sec.

When the data for both initiators and receivers were cast into preceding act-following act transition matrices some acts were infrequent enough to result in more than 20% of the matrix cells having values less than 5. This contravenes a requirement that no more than 20% of matrix cells should be less than 5 for further statistical analysis (Fagen and Young 1978). Further, Fagen and Young state that a minimum number of transitions of $5r^2$ (r = repertoire size) should be obtained before chi-square transition analysis. Because my sample size wqs only slightly above this value for both initiator and receiver data, the original 14 x 14 matrices were reduced to 7 x 7 matrices by consolidating acts of rare occurrence or those which were part of or closely associated with more prominent acts.

Facial Rub-Leg Push combines facial contact and foreleg push since the latter appeared to be a vigorous extension of facial contact.

Facial Contact - Stands directly facing partner; begins with nasal contact to the nasal region of the partner; the mouth is slightly open and the lips hang loose; progresses to a head nuzzling of the neck area immediately below partner's head; head and neck are seldom held below the horizontal.

Foreleg Push - Sits or stands facing partner; often nasal contact or more general head contact with partner; suddenly lunges forward pushing one or both forelegs onto the neck and/or chest region of the partner.

Rear-Grapple-Wrestle combines rearing through positioned over, all of which involve much body contact. Also, some of the acts (e.g., inhibited bite, bite and hold) were commonly seen as components of more general acts such as positioned over and positioned underneath.

Rearing - Stands facing partner; suddenly rises up on hindlegs with the forelegs partially folded into the body; the head and neck are angled slightly forward, and the head is pointed slightly downward; the mouth is slightly open and the lips hang loose; no contact with the partner is made; drops back to quadrupedal position if the partner does not rear.

Rear and Contact - Stands facing partner; suddenly rises up on hindlegs and pushes forward with forelegs onto the chest region of partner; or it wraps one or both forelegs around the neck and/or shoulder region in attempt to force the partner downward and sideways; this behavior is always mutual.

Positioned Underneath - Can be lying on back or side; partner is either standing over or lying across; usually accompanied by much facial contact and mutual mouthing of the rostral area.

Inhibited Bite - Grasps a part of partner, usually the neck or shoulder region; jaws are not closed; can be in either a lying or standing position.

Bite and Hold - Seizes an extremity of partner such as the ear or paw and bites down while at the same time pulling back with head; can be either lying or standing.

Positioned Over - Either lying or standing over partner; usually much facial contact and mutual mouthing of the rostral area.

Forward Advance - Stands facing partner; either nasal contact with partner or with head beside partner's, sometimes with contact; walks slowly forward and partner walks backward; head and neck above horizontal.

Backward Retreat - Stands facing partner, either nasal contact with partner or with head beside partner's, sometimes with contact; walks slowly backward and partner walks forward.

Walk Away and Flee were combined since they signified withdrawal by one of the interactants.

Walk Away - Suddenly turns and walks away at a normal gait from partner; does not look back unless pursued by partner.

Flee - Turns and runs away from partner; may run up to 100 m from partner.

Rush - Suddenly runs toward partner; head and neck below horizontal; contact may occur or the rush may be terminated before contact.

Face - Stands oriented directly toward partner; watches partner intently with head and neck either at horizontal or slightly below; there may be some circling about by both bears but both continue to watch one another intently.

G-tests of goodness of fit were applied to the 7 x 7 transition matrices for both initiators and receivers (Sokal and Rohlf 1969). The data were now well above $5r^2$; however, 30% of the cells were still less than 5. The results of the G-tests were highly significant ($P < 0.001$) for both initiators and receivers, meaning that some acts followed others more often than expected by chance. A graphical approach to the transition data was taken in which only transition values representing greater than 2% of the total number of transitions for both initiator and receiver were included on a kinematic graph. Each graph represents 85% of the total number of transitions.

During field observations I gained the impression that bouts commonly progressed through phases; an introductory phase followed by a more vigorous decision phase and a final outcome phase. Part of the analysis deals with this "a priori" approach to bout structure. All bouts were divided into three equal parts based on time. The number of occurrences of an act in each of the three phases for all 73 bouts was tallied and the proportion expressed as a percentage of the total number of occurrences of each act in all bouts.

RESULTS

A total of 73 bouts between adult males were recorded in this study. Fifty-four of these involved one marked individual and 19 involved two marked individuals. A total of three marked bears and approximately seven unmarked bears were involved.

Bout duration varied considerably ($\bar{X}$ = 221 sec, S.E. = 26 sec), and the acts comprising bouts also varied in duration (Table 1).

TABLE 1

Mean duration and coefficient of variation (C.V.) of bout acts

BOUT COMPONENT	INITIATOR			RECEIVER		
	N	Mean duration (sec)	C.V.(%)	N	Mean duration (sec)	C.V.(%)
Facial Rub-Leg Push	233	10.6	90.1	224	10.9	88.4
Rear-Grapple-Wrestle	155	42.1	180.8	146	44.5	174.1
Forward Advance	78	19.6	99.0	38	12.3	93.0
Backward Retreat	35	12.3	97.0	75	15.4	120.0
Rush	9	6.3	30.6	4	4.5	64.2
Walk Away-Flee	28	8.1	63.3	67	14.8	80.9
Face	281	17.5	103.2	261	17.5	109.0

Acts of short duration have lower coefficients of variation, indicating less variability, than the acts of longer duration. Rear-Grapple-Wrestle, a vigorous act involving much physical contact, was of longest duration and highest variability. Acts such as Rush and Walk Away-Flee were relatively brief and less variable.

The frequency and duration of some acts differed significantly between initiators and receivers. Forward advance was more frequent for initiators than receivers ($X^2 = 13.8$, $P < 0.001$), and Backward Retreat was greater for receivers than initiators ($X^2 = 16.8$, $P < 0.001$); these differences are expected given the mutuality of these two acts. Walk Away-Flee occurred more often in receivers than initiators ($X^2 = 16.0$, $P < 0.001$). The durations of Forward Advance and Rush acts were significantly longer for initiators than receivers (Mann-Whitney test, $P < 0.001$). Durations of Backward Retreat and Walk Away-Flee were significantly longer for receivers than initiators (Mann-Whitney test, $P < 0.001$).

Some acts had a high degree of mutuality (Table 2). The table values represent act pairs at each initiator or receiver transition or at mutual transitions. Mutual transition accounts for the large majority of transitions (89.5% for both initiators and receivers). Acts with the greatest initiator-receiver mutuality are Facial Rub-Leg Push, Rear-Grapple-Wrestle, Forward Advance and Backward Retreat, and Face.

Figures 1 and 2 outline the essential differences between bout initiators and receivers. The area of each box is proportional to the total number of acts. Arrow width is proportional to the total number of transitions. Both initiators and receivers have a major axis formed by Facial Rub-Leg Push, Face, and Rear-Grapple-Wrestle. Face was the

TABLE 2

Acts of initiators and receivers at each transition. A transition refers to either mutual changes in behavior or only one bear changing behavior.

INITIATOR	RECEIVER						
	Facial Rub-Leg Push	Rear-Grapple-Wrestle	Forward Advance	Backward Retreat	Rush	Walk Away-Flee	Face
Facial Rub-Leg Push	153 (18.4%)	7 (.8%)	1 (.1%)	1 (.1%)	0	0	16 (1.9%)
Rear-Grapple-Wrestle	2 (.2%)	151 (18.2%)	0	1 (.1%)	0	0	10
Forward Advance	0	0	0	70 (8.4%)	0	23 (2.8%)	1 (.1%)
Backward Retreat	0	1 (.1%)	35 (4.2%)	0	0	2 (.2%)	0
Rush	0	0	1 (.1%)	0	0	7 (.8%)	1 (.1%)
Walk Away-Flee	0	0	4 (.5%)	0	2 (.2%)	1 (.1%)	23 (2.8%)
Face	8 (1.0%)	3 (.4%)	3 (.4%)	4 (.5%)	2 (.2%)	58 (7.0%)	241 (29.0%)

FIGURE 1. Two-act sequences for initiators of bouts (N = 819)

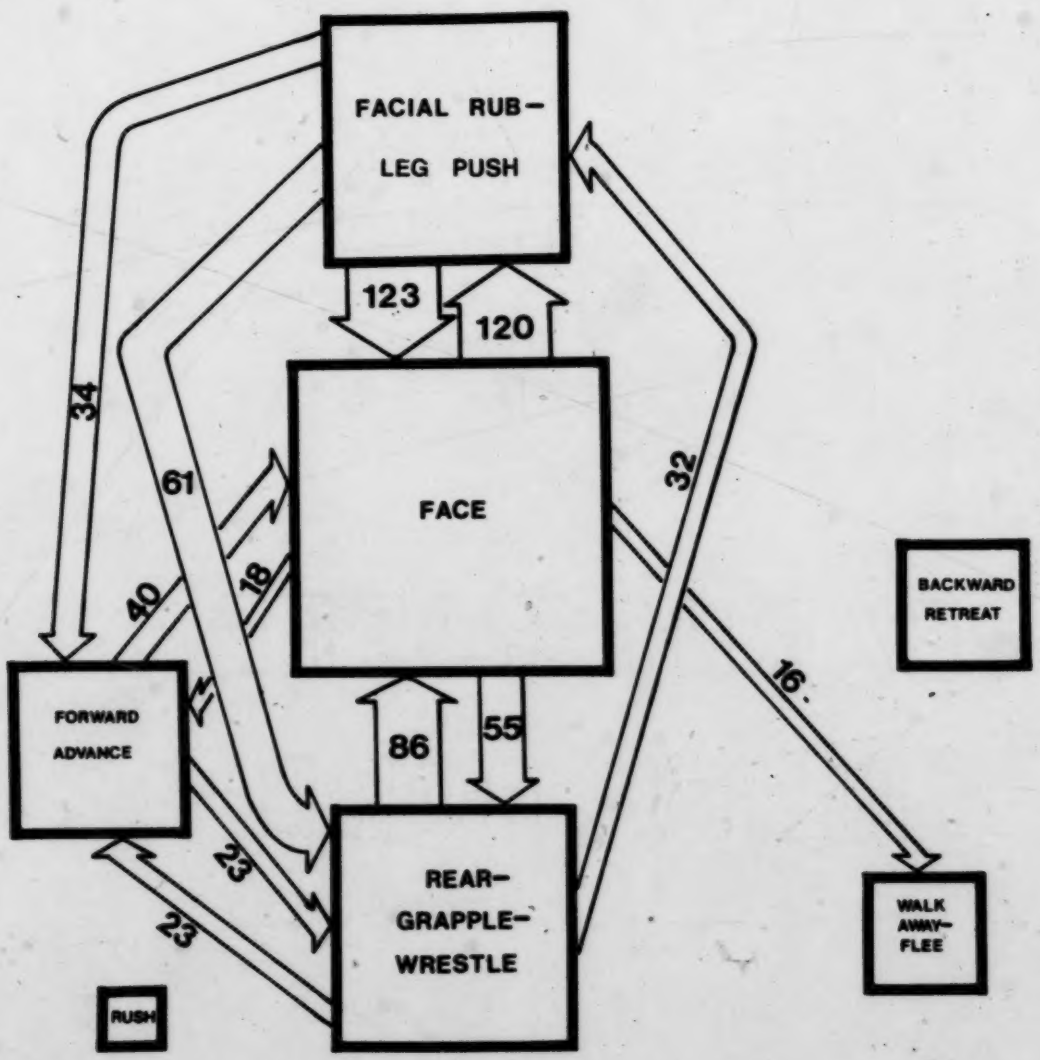
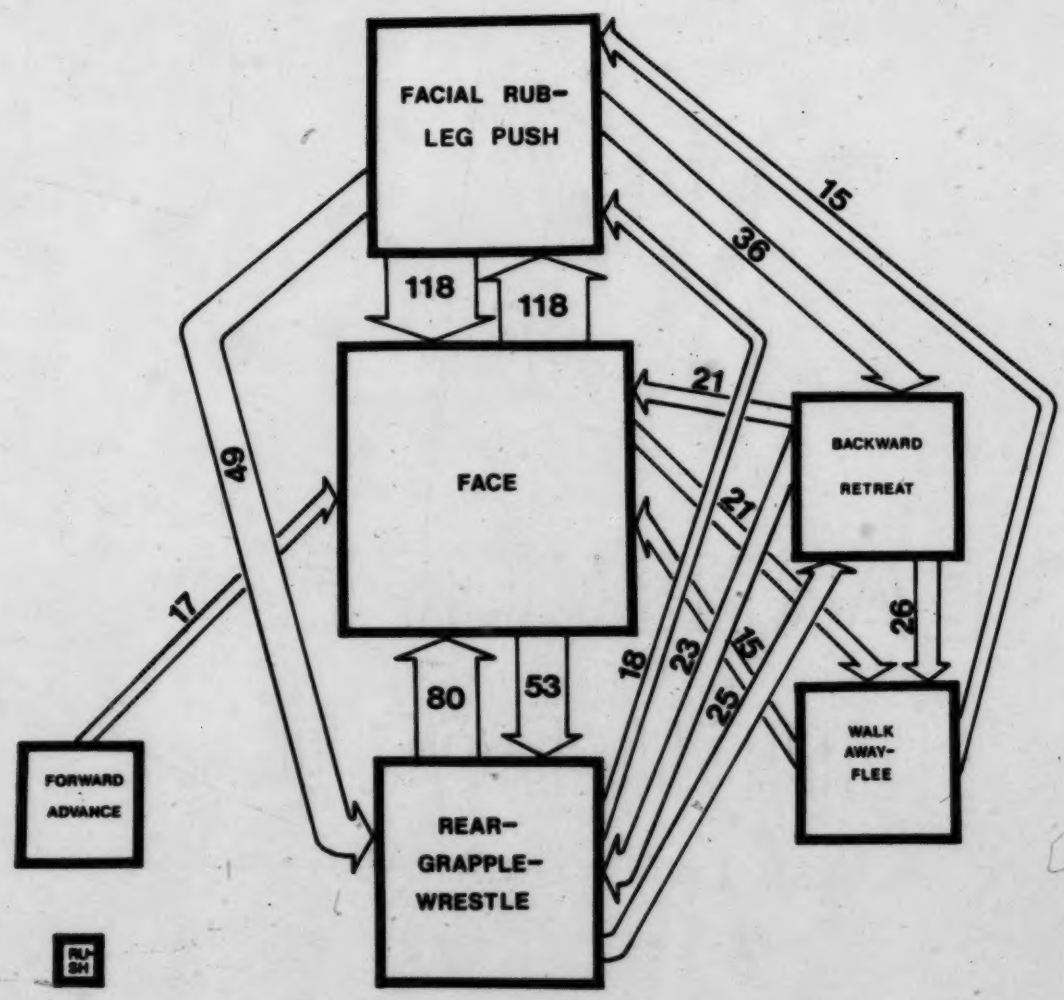

FACIAL RUB–
LEG PUSH
123
120
34
61
32
FACE
40
18
BACKWARD
RETREAT
16
FORWARD
ADVANCE
86
55
23
23
REAR–
GRAPPLE–
WRESTLE
WALK
AWAY–
FLEE
RUSH

FIGURE 2. Two-act sequences for receivers of bouts (N = 812)


FACIAL RUB-
LEG PUSH
15
36
118
118
FACE
21
BACKWARD
RETREAT
64
21
17
26
18
23
25
80
53
FORWARD
ADVANCE
WALK
AWAY-
FLEE
REAR-
GRAPPLE-
WRESTLE

most common act observed in both initiators and receivers. Initiators differed from receivers by the predominance of Forward Advance, and by less frequent Backward Retreat and Walk Away-Flee. Another difference is that initiators used Rear-Grapple-Wrestle more frequently after Facial Rub-Leg Push (then switched back to Facial Rub-Leg Push immediately afterward). Initiators and receivers are similar in that branching from the three main axis acts to other acts is not strongly patterned.

Figures 1 and 2 are based on data pooled from all bouts. When examined individually, some bouts were found to lack one or more of the seven acts (Table 3). All bouts contained Facial Rub-Leg Push by both participants, and most contained Face as well. Major differences between initiators and receivers are that initiators used Forward Advance in more bouts than Backward Retreat (45% vs. 30%) and vice versa for receivers (32% and 46%). In addition, Walk Away-Flee was performed in more bouts by receivers than initiators. The rare act Rush was performed in more bouts by initiators than receivers.

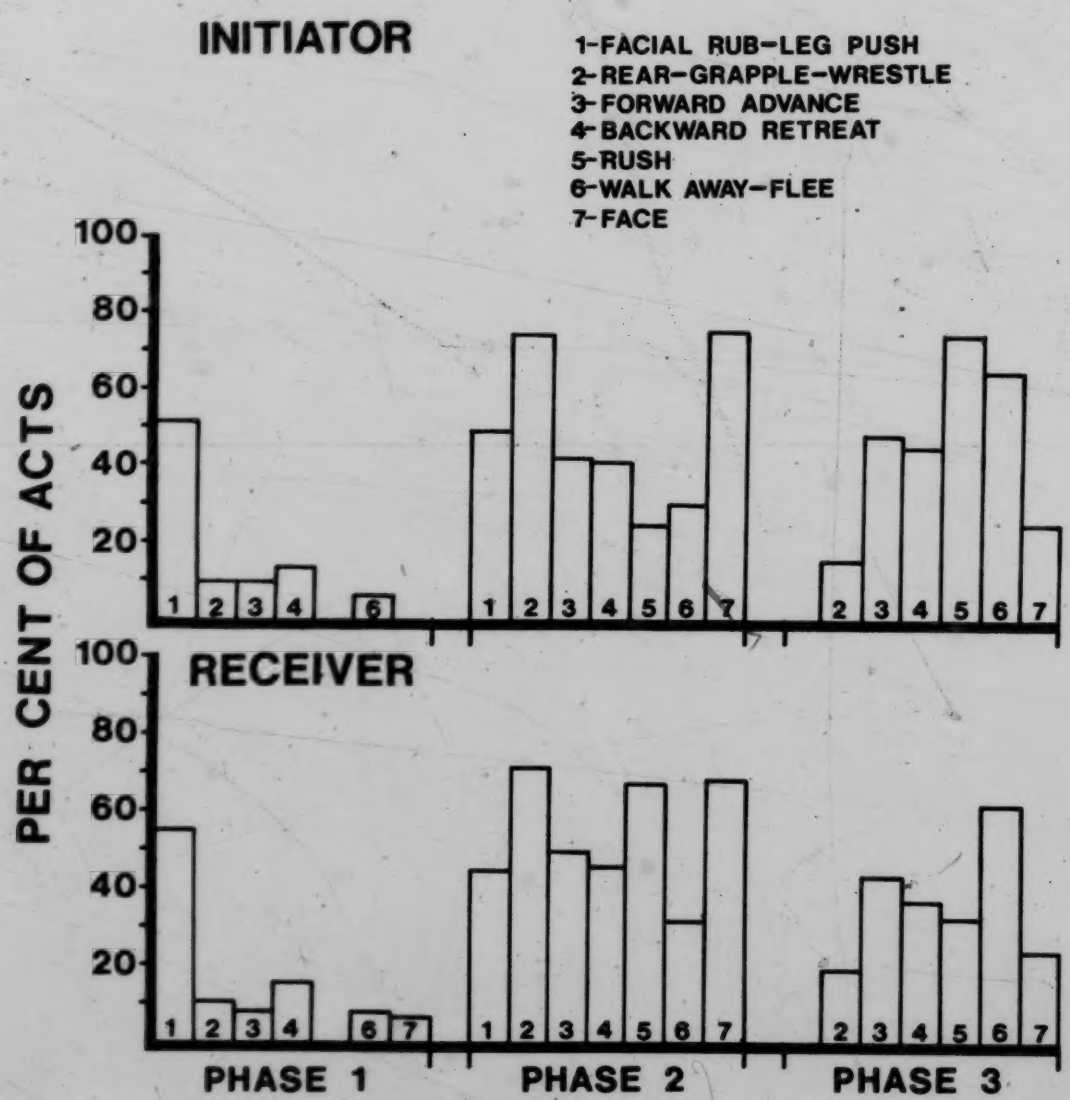
Figure 3 illustrates a generalized bout structure for both initiators and receivers. Only Facial Rub-Leg Push was frequent in phase 1. In phase 2, incidence of Facial Rub-Leg Push decreased slightly but more vigorous acts such as Rear-Grapple-Wrestle, Forward Advance, Backward Retreat and Face became common. In phase 3, Facial Rub-Leg Push is absent and incidence of Rear-Grapple-Wrestle and Face decreased. Rush increased in phase 3 for initiators only. Walk Away-Flee increased in phase 3 for both initiators and receivers. In short, phase 1 is an introductory period characterized by much anterior contact. Phase 2 is an escalation where participants use more vigorous acts in an attempt to

TABLE 3

Proportion of the 73 bouts in which each of the seven acts was present (for initiators and receivers)

	PROPORTION OF BOUTS						
	Facial Rub-Neck Cross	Rear-Grapple-Wrestle	Forward Advance	Backward Retreat	Rush	Walk Away-Flee	Face
INITIATOR	100%	58%	45%	30%	11%	35%	100%
RECEIVER	100%	57%	32%	46%	4%	53%	95%

FIGURE 3. Proportion of acts in phases 1-3 for initiators and receivers. The total of all phase proportions for each act is 100%.


INITIATOR
1-FACIAL RUB-LEG PUSH
2-REAR-GRAPPLE-WRESTLE
3-FORWARD ADVANCE
4-BACKWARD RETREAT
5-RUSH
6-WALK AWAY-FLEE
7-FACE
PER CENT OF ACTS
100
80
60
40
20
RECEIVER
PHASE 1
PHASE 2
PHASE 3

force off balance and pin to the ground an opponent, or to counter such attempts. Phase 3 is similar to phase 2 except that the termination act, walk away-flee, is more prevalent. Sixteen percent and 37% of bouts for initiators and receivers respectively were terminated by walk away-flee.

Bouts did not always display acts diagnostic of the three phases discussed above. Eighty percent of all bouts showed acts diagnostic of phase 2, and 53% continued on to phase 3. Bouts that terminated immediately after acts diagnostic of phase 2 generally ended in forward advance-backward retreat followed by a period of facing. A small fraction of bouts (6%) terminated abruptly prior to acts diagnostic of phase 2. They were characterized by much facial rub-leg push, then terminated by a 30 sec period of facing.

DISCUSSION

Adult male bouts are variable in both overall duration and the duration of their constituent acts. The results of this study, however, suggest that bouts are predictable and structured to some extent. The mutuality of certain acts and the dual nature of initiator-receiver transitions indicate that participants responded to one another in a predictable manner. A sequential structuring is indicated by a major axis of three acts (Figs. 1 and 2) from which branch acts that are more specific to either initiators or receivers. Initiators use the aggressive act forward advance while receivers use less aggressive acts such as backward retreat and walk away-flee. The phase analysis results suggest that some acts are observed more frequently than others at

certain points in a bout, further indicating the structured nature of bouts. This structure is generalized however, because some acts are not present in all bouts (Table 3).

That initiators and receivers differ in the frequency and duration of acts used in bouts is largely explainable by the mutuality of certain acts. Initiators use aggressive acts more often, and the durations of these acts are longer than those for receivers. Receivers respond with less aggressive acts more often and the durations of these acts are longer than those for initiators.

It is generally thought that all forms of play occur only when essential biological needs have been temporarily satisfied (Bekoff 1975). In a related paper (Latour 1980) I discuss the non-competitive situation of polar bears spending the ice-free season along the west coast of Hudson Bay. These bears feed very little for 4-5 months, and reproductive behavior is absent since they breed on the sea ice at a different time of the year. I consider the bouts observed in this study between adult male polar bears to be social play, for several reasons. First, the pre-requisite that all biological needs be satisfied before play can occur appears to be met in this study (see Latour 1980). Second, the restrained nature of certain acts such as inhibited biting and grappling (versus their potentially damaging counterparts of biting and clawing) as well as the almost complete lack of superficial wounding are in agreement with current concepts on the physical nature of social play (Bekoff 1972). Third, the non-vocal nature of bouts observed in this study agrees with findings on play in other species of ursids. Although data on polar bears are lacking, findings for other species indicate the

the silent nature of social play versus more serious agonistic encounters (Henry and Herrero 1974; Pruitt 1976; Rogers 1977). Particularly noteworthy was the absence of the "chuffing" vocalization described by Wemmer et al. (1976) in polar bears that is common during stressful interactions among polar bears (Jonkel 1970; Latour, pers. obs.) and other ursids. Finally, studies on juvenile social play in other ursid species (Henry and Herrero 1974; Pruitt 1976) describe acts that are similar to those used by adult male polar bears in this study (e.g., the inhibited nature of biting and restrained use of the forelegs). One discrepancy between the literature and my results was the absence of sexual mounting in social play between adult male polar bears. Such homosexual acts are seen occasionally in the social play of juvenile ursids (e.g., black bear, *Ursus americanus*) (Henry and Herrero 1974; Pruitt 1976). Play between adult polar bears and between lone subadults dispersed and hunting on sea ice has been reported (Stirling, pers. comm.), but rarely. In the High Arctic, play between littermates, especially those under one year of age, has been observed frequently (Stirling, unpubl. data).

Fagen (1974) and Bekoff (1975) review both the structuralist and functionalist approaches to play behavior. Structuralist considerations have centered on the temporal sequencing of acts comprising play and how the arrangement of these acts compares to their arrangement in more serious interactions. Early conclusions were that play is a completely random series of acts. With the advent of more rigorous analysis it was shown that juvenile social play, at least in some species, has a definite temporal structure (Poole and Fish 1975).

I have no data with which to make quantitative comparisons between social play and more serious interactions as some workers have done (Hill and Bekoff 1977). As discussed earlier, structure in the social play of adult male polar bears is suggested by the phase differences in frequency of acts, the marked initiator-receiver differences indicating an element of predetermined advantage held by initiators and the main three-act axis for both initiators and receivers. Furthermore, many bouts terminated with distinct acts, contradicting the conclusions of some non-structuralist authors who state that play lacks distinct termination signals (Ewer 1968).

Functionalist hypotheses concerning play are numerous, and include such interpretations as release of excess energy, practice, innovation and socialization. The excess energy theory is probably the least plausible because of contradictory results obtained in the few studies designed to examine excess energy and its effects on play (see Bekoff 1975). The possible socialization function of play has been examined in juveniles from the standpoint of integration into a social unit (e.g., a primate troop), dominance establishment, and refinement of communication. Practice and innovation have been considered in the context of juveniles using play to increase the precision and diversity of social interaction. Clearly, practice-innovation and socialization interrelate closely in the overall socialization process of juvenile animals.

Social play between adults has been reported only occasionally in the literature (see Fagen 1977), and these accounts usually deal with highly social species. For more solitary species, MacDonald (1977) reported play between adult female red foxes, but these were members of

the same kin group. Roger's (1977) description of play in adult male black bears concentrated at dumps is more comparable to my study. Although no quantitative analysis was done he concluded that these individuals were probably unrelated and that they had come from an extensive area to use a concentrated food source. Egbert and Stokes (1976) reported social play in male brown bears, 4.5-8.5 years of age, concentrated along a salmon stream. They did not observe social play in males older than 8.5 years. There was a higher incidence of social play in years when salmon were abundant than in years when they were not.

What could be the possible function of play behavior in adult male polar bears? The practice-innovation, and socialization set of hypotheses is attractive from the standpoint of adult males using play to refine patterns of interaction used in more serious agonistic interactions that occur especially during breeding. This idea could only be tested by gathering data on serious encounters and comparing these to data on play behavior. Ideally, data should be collected on the same individuals for both cases. If an individual's sequence of play acts used in forcing an opponent to withdraw was similar to its sequence of acts used in "successful" agonistic interaction, where success could be gaining access to estrous females or defending a seal kill, then practice-innovation gained through play might be advantageous.

Ewer (1968) and Eibl-Eibesfeldt (1966, 1970) discuss ritualized combat as tests of strength used in determining dominance hierarchies and defending territories. In a theoretical approach Parker (1974) discusses fighting behavior in terms of opponent assessment or as he terms it, their "resource holding potential." He cites several examples of disputes in which body size is the main factor in determining

outcomes, and states that body size, along with strength, weaponry and experience, all seem involved in resource holding potential. Maynard Smith and Parker (1976) discuss asymmetry in contests (e.g., size differences) and the ability of individuals to assess one another without physical contact. Although the bouts described in this study would appear to fall short of ritualized combat, perhaps social play between adult males can be interpreted in a similar fashion. The vigorous acts of phase 2 suggest a "testing" function. Perhaps an adult male can develop the ability to assess a conspecific's fighting capability using visual cues such as body size (Geist 1971) and nuances of pre-contact behavior. Social play would provide the exposure to a variety of conspecifics upon which this ability could be based.

Geist (1974) and Brown (1975) point out that large body size in males relative to females, a shorter life expectancy than females, and a longer growth period are indicators of intense male sexual selection. Although caution in equating sexual dimorphism and sexual selection is required (Ralls 1977), extensive population ecology studies of polar bears (Stirling et al. 1975, 1977; Kingsley 1979) show that adult male polar bears satisfy the above criteria, suggesting that sexual selection may occur in this species. Competition between adult males is intensive during the breeding season, as evidenced by the frequent grouping of adult males around single, estrous females, fights between males and the increased incidence of superficial wounding in males at that time (pers. obs.). Accurate opponent assessment and prudent retreat could prove advantageous in avoiding serious injury from superior opponents (Clutton-Brock et al. 1979). It is unlikely, however, that play bouts observed in concentrated adult male polar bears function as immediate determiners

of dominance because of the dispersed nature of these same individuals during most of the year. Also the likelihood of enough adult males remaining on the study area long enough to form stable dominance relationships is small (Latour 1980).

Data on subadult social play could shed light on its importance in preparation for agonistic interactions in adult life. A gradient may exist between subadult play and adult agonistic interactions in which the same acts are used in both instances but the ordering of these acts becomes more predictable with age. Or, some acts may appear or disappear with age. The limited data I obtained on subadult bouts suggest that the use of certain acts such as Rear-Grapple-Wrestle differs in frequency, duration and sequencing as compared to adult male bouts.

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THESIS DISCUSSION

Polar bears dispersed on the pack ice of Hudson Bay come ashore along the west coast of Hudson Bay during late June to late July. Aggregations occur each year at certain locations along the coast. I found that the aggregation at Cape Churchill, Manitoba, had both spatial and behavioral organization. Adult males, subadult males and subadult females each frequented different regions of the study area. Adult males associated more closely with one another than did either subadult males or subadult females. The only significant difference in behavior between the three age/sex classes either in overall time budget (i.e., active, inactive, social behavior) or in specific social behavior (i.e., social time budget and social composition) was that subadult females were the most active. Adult males did spend more time in contact than did the other two classes and a larger amount of adult male social behavior was composed of contact behavior. Bears tended to interact with members of their own age/sex class; this may reflect the spatial segregation of the three age/sex classes.

Would not this essentially solitary species be expected to spend the ice-free season dispersed along the coast with individuals inactive and ignoring one another? My data show that although individuals are mainly inactive there is increased sociability compared to when they are hunting on the sea ice. Increased sociability during this slack, non-competitive period in their annual cycle may allow individuals to better assess unfamiliar conspecifics at other times of the year when intra-specific competition is more intense.

Analysis of social play between adult male polar bears enabled closer examination of the above idea. Play bouts have a degree of structure and predictability. The most vigorous acts, designed to force an opponent off balance, generally occur in the middle of a bout and are often followed by one or more withdrawing acts. Bouts therefore may function as a means of assessing strength and fighting capability during which an individual may learn its chances of success (i.e., forcing an opponent to withdraw) against various sized conspecifics. This may be advantageous at times of more direct intraspecific competition such as thwarting other adult males from an estrous female or fending off interlopers from a seal kill. Knowing when to escalate a defense or offense and when not to could be desirable in avoiding serious injury from superior opponents (see Parker 1974; Clutton-Brock et al. 1979).

There are several avenues of research that could be followed vis-à-vis this study. For example, polar bear density on the study area evidently varies from year to year. During a preliminary observation period in 1976 there were more bears on the study area than in either 1977 or 1978. Observations made during a high density year may elucidate the relationship between density and distribution, especially the tendency, detected in this study, of age/sex classes to accommodate one another at higher density by decreasing interindividual distance rather than spacing themselves out over more area. In addition, the possible effects of higher density on interclass interactions could be examined.

Data on subadult social play could be compared with that for adult males. Is subadult social play structured differently than adult male social play and is it more, or less, predictable? Does subadult

social play lack certain acts present in adult male social play? The small amount of data I obtained on subadults suggests that their bouts are longer, the majority lack a clear-cut outcome and the vigorous acts diagnostic of phase 2 occur less frequently. More data would shed light on the ontogeny of social play and its importance to the social relations of both adults and subadults. Indeed, aggregations of polar bears such as those at Cape Churchill provide a unique opportunity to examine the ontogeny of play, especially if play between adults is as rare as the literature to data indicates.

The introduction of a large food source (or sources) to the study area (e.g., whale carcasses obtained from white whale (*Delphinapterus leucas*) hunters at Churchill townsite), although posing logistic and esthetic problems, could be a means of testing several of the hypotheses proposed in this thesis. Would competition at food sites be expressed by intense aggressive interactions? Would the general age/sex class segregation found in this study become more marked when competition becomes a factor? How do obviously aggressive interactions compare with social play in terms of structure, variability and outcome?

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